Forage and migration habitat of loggerhead (Caretta caretta) and olive ridley (Lepidochelys olivacea) sea turtles in the central North Pacific Ocean

JEFFREY J. POLOVINA, 1,* GEORGE H. BALAZS, EVAN A. HOWELL, DENISE M. PARKER, MICHAEL P. SEKI AND PETER H. DUTTON³

¹Pacific Islands Fisheries Science Center, National Marine Fisheries Service, NOAA, 2570 Dole Street, Honolulu, HI 96822-2396, USA

²Joint Institute for Marine and Atmospheric Research, University of Hawaii, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA ³Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Dr., La Jolla, CA 92037, USA

ABSTRACT

Satellite telemetry from 26 loggerhead (Caretta caretta) and 10 olive ridley (Lepidochelys olivacea) sea turtles captured and released from pelagic longline fishing gear provided information on the turtles' position and movement in the central North Pacific. These data together with environmental data from satellite remote sensing are used to describe the oceanic habitat used by these turtles. The results indicate that loggerheads travel westward, move seasonally north and south primarily through the region 28-40°N, and occupy sea surface temperatures (SST) of 15-25°C. Their dive depth distribution indicated that they spend 40% of their time at the surface and 90% of their time at depths <40 m. Loggerheads are found in association with fronts, eddies, and geostrophic currents. Specifically, the Transition Zone Chlorophyll Front (TZCF) and the southern edge of the Kuroshio Extension Current (KEC) appear to be important forage and migration habitats for loggerheads. In contrast, olive ridleys were found primarily south of loggerhead habitat in the region 8-31°N latitude, occupying warmer water with SSTs of 23– 28°C. They have a deeper dive pattern than loggerheads, spending only 20% of their time at the surface

and 60% shallower than 40 m. However, the three olive ridleys identified from genetics to be of western Pacific origin spent some time associated with major ocean currents, specifically the southern edge of the KEC, the North Equatorial Current (NEC), and the Equatorial Counter Current (ECC). These habitats were not used by any olive ridleys of eastern Pacific origin suggesting that olive ridleys from different populations may occupy different oceanic habitats.

Key words: loggerhead turtle, olive ridley turtle, pelagic habitat, turtle migration

INTRODUCTION

While it is known from incidental hookings by fishing gear that loggerhead (Caretta caretta) and olive ridley (Lepidochelys olivacea) sea turtles occupy oceanic regions, far from coastal habitats, their forage and migration habitat in these oceanic regions have not been well described. In the Pacific, loggerheads travel between their nesting beaches in Japan and Australia and foraging habitat in the eastern Pacific. Genetic analyses of the loggerheads off Baja California concluded that 95% came from Japanese nesting beaches and 5% from nesting colonies in Australia (Bowen et al., 1995). Data on the location and movement of nine loggerhead turtles tracked during 1997–98 in the central North Pacific by satellite telemetry indicated that oceanic fronts, particularly the chlorophyll front known as the Transition Zone Chlorophyll Front (TZCF), provided mid-oceanic forage and migration habitat for juvenile loggerheads in the central Pacific (Polovina et al., 2000, 2001).

Olive ridleys are regarded as the most abundant sea turtles in the world with the largest nesting population occurring in the Indian Ocean along the north-east coast of India. The second largest nesting population is located in the eastern Pacific, along the west coasts of Mexico and Central America (National Marine Fisheries Service and US Fish and Wildlife Service, 1998). Genetic analysis has shown that olive ridleys from both western and eastern Pacific nesting populations

^{*}Correspondence. e-mail: jeffrey.polovina@noaa.gov Received 25 February 2002 Revised version accepted 31 December 2002

forage in the central North Pacific (Dutton et al., 1999).

During 1997–2001 observers on Hawaii-based longline fishing vessels attached Argos satellite-linked transmitters to juvenile loggerhead and juvenile olive ridley turtles caught by longline gear. We investigated the oceanic habitat and movements of these two species of turtles based on satellite telemetry of 26 loggerheads, including nine loggerheads used in Polovina *et al.* (2000), and 10 olive ridleys together with information on their oceanic habitats obtained from satellite remotely sensed and ship-based oceanographic data.

DATA AND METHODS

The Argos-linked Telonics (Mesa, AZ, USA) ST-10 or ST-18 position transmitters were attached to 32 turtles. Additionally, two loggerhead and two olive ridley turtles were instrumented with a Wildlife Computer (Redmond, WA, USA) Argos-linked satellite transmitter with dive recorder capabilities (SDR-T10). This transmitter provides, in addition to position data, three frequency distributions for each of four 6-h time periods. One frequency distribution presents the distribution of time spent in each of 14 preset depth bins. The second frequency distribution contains the distribution of the duration of each dive. The third frequency distribution contains the distribution of the maximum depth for each dive. The 6-h periods were 21:00-03:00, 03:00-09:00, 09:00-15:00, and 15:00–21:00 hours, Hawaii standard time. The lower range of the depth bins (in meters) were: 1, 3, 5, 10, 15, 25, 35, 50, 60, 75, 100, 125, 150, 150+. Personnel of the National Marine Fisheries Service's Observer Program attached transmitters to the turtles onboard commercial fishing vessels. They used fiberglass cloth and resin to attach the transmitter as recommended by Balazs et al. (1996).

The Argos transmissions ranged from 30 to 458 days and spanned the time period from January 1997 to August 2001 for a total of 2470 transmission-days. Transmitters had 3 duty cycles, i) 2 h on, 4 h off, ii) 12 h on, 48 h off, iii) 24 h on, 24 h off. The reasons the transmissions ended are not known but they could have been caused by failure or detachment of the transmitter, depletion of battery power, or the death of a turtle. All loggerheads used in this study were determined by genetic analysis to have come from Japanese nesting beaches. Genetic analyses of nine of the tracked olive ridleys showed that six (67%) came from eastern Pacific nesting beaches and the remaining three came from the western Pacific. Three of the

loggerheads [83, 83 and 81 cm straight carapace length (SCL)] and two of the olive ridleys (66 and 61 cm SCL) may have been large enough, based on their carapace lengths, to be sexually mature; however, all the other turtles were likely immature.

The physical and biological environmental data used to describe the environment at and around the migrating loggerheads and olive ridleys are sea surface temperature (SST), surface chlorophyll a concentration, and geostrophic current. The SST data were multichannel SST (MCSST) from the University of Miami, with weekly temporal resolution and onetenth of one degree of longitude and latitude spatial resolution. Global comparisons between MCSST and ship-based temperature measurements indicated that MCSST is 0.3-0.4°C lower than ship-based temperature with cross-correlations ranging from +0.3 to +0.7 (McClain et al., 1985). Chlorophyll a concentration was estimated from the Sea-viewing Wide Fieldof-view Sensor (SeaWiFS) version 2 data (O'Reilly et al., 1998). The data resolution was monthly, September 1997-August 2001, at 0.088° latitude and longitude. The accuracy of SeaWiFS chlorophyll estimates were within 30-50% of ship-based observations (McClain et al., 1998). Geostrophic currents were computed from satellite altimetry data from TOPEX/Poseidon with 10-day and 0.5° latitude and longitude resolution (Polovina et al., 1999). Comparisons between current speed determined from an acoustic Doppler current profiler along TOPEX/ Poseidon track lines around the Hawaiian Archipelago agreed with estimates from TOPEX/Poseidon to within a few cm s⁻¹ (Mitchum, 1996).

The environmental data were linked to the turtle's position by spatial interpolation between grid points. Specifically, a cubic polynomial was used to estimate the environmental data at and around all turtle locations from the observed environmental grid. A computer routine, 'grdtrack,' within the software package Generic Mapping Tools (GMT) (http://gmt.soest. hawaii.edu) was used for the interpolation. Finally, data on subsurface temperature and chlorophyll in the region occupied by loggerhead and olive ridley turtles were obtained from two shipboard oceanographic transects.

A series of location accuracy classifications was assigned to the reported turtle positions by Argos, and then computed as a function of the number and configuration of satellites and number of transmissions received for each position calculation. In our subsequent analyses, when there were multiple Argos positions at different times of the day for the same turtle, we selected the most accurate position. If two

positions had the same Argos accuracy classification, we selected the position closest to noon. For the set of all of our daily turtle positions, Argos estimated that the distance between the reported and true positions was <1 km for 36% of the positions and at least 1 km for 43% of the positions. The remaining 21% did not have sufficient data to be classified by Argos but are believed to have been within several kilometers of their true positions. Turtle speeds were based on movements between the successive daily positions, and hence represent minimum straight line distances between the daily position estimates.

RESULTS

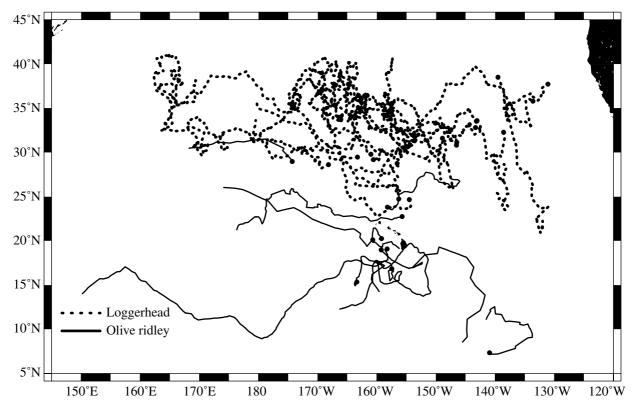
The spatial distribution of all track lines for the 36 turtles released with transmitters after capture in the Hawaii-based longline fishery spanned an area from latitude 6–41°N and longitude 130°W–150°E (Fig. 1). Little spatial overlap existed between the two species, as loggerheads were predominately north of about 28°N occupying the northern portion of the Subtropical Gyre and the Transition Zone, while the olive ridleys were generally south of 28°N in the Subtropical

Gyre and the equatorial region (Fig. 1). All the loggerheads traveled westward with the exception of two on the eastern edge of the area that traveled southeast, while olive ridleys exhibited both eastward and westward movements.

To examine the distribution of each species of turtle, latitude–frequency distributions were constructed from the daily loggerhead positions pooled within each quarter over all years. The quarterly latitude–frequency distributions for loggerheads indicated that they occupied the southern portion of their range during the first and second quarters and the northern portion of their range during the third and fourth quarters (Fig. 2). The quarterly latitude–frequency distributions for olive ridleys showed a broader latitude range than for loggerheads, primarily from 8–31°N with a suggestion that they too may seasonally move north and south (Fig. 2).

To examine the SST ranges occupied by each species of turtle, quarterly SST–frequency distributions were constructed by linking daily turtle positions with remotely sensed SST at each daily position and then pooling the SSTs within each quarter over all the years. Olive ridleys primarily occupied a 5°C SST

Figure 1. Track lines of 26 loggerhead (dashed) and 10 olive ridley (solid) turtles based on daily Argos reported positions from the period 1997–2001. Solid dots mark the start of each track line.



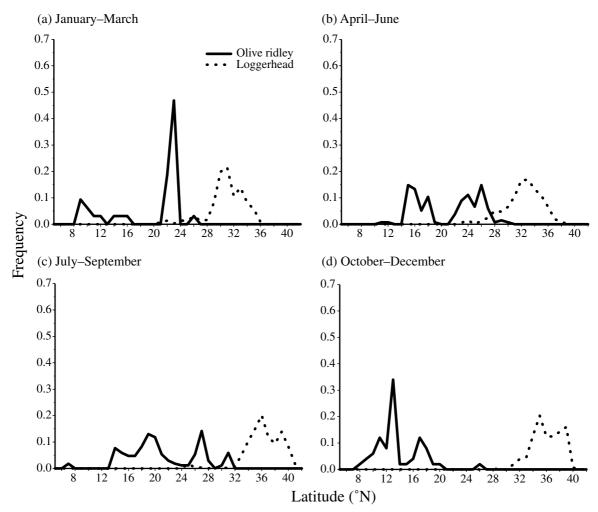


Figure 2. Quarterly latitude-frequency distributions for loggerheads (dashed) and olive ridleys (solid), pooled for 1997–2001.

range, 23–28°C during all quarters, but within that range they appeared to be found centered at 24 and 27°C (Fig. 3). Loggerheads occupied cooler water and covered a broader 10°C SST range, 15–25°C, occupying cooler temperatures in winter and spring and warmer temperature in the summer (Fig. 3). Many of the turtles remained in very narrow SST ranges during their entire transmission time, while others occupied SSTs throughout the broader ranges shown for pooled quarterly SST–frequency distributions.

A relationship between loggerhead habitat and the sharp gradient in surface chlorophyll, termed the TZCF, has been observed (Polovina *et al.*, 2000, 2001). The TZCF represents the boundary between the stratified low surface chlorophyll (<0.15 mg m⁻³) waters of the Subtropical Gyre and the high surface chlorophyll (>0.3 mg m⁻³) vertically mixed waters in the Transition Zone and Subarctic Gyre. A chloro-

phyll level of 0.2 mg m⁻³ was used to locate this feature (Polovina et al., 2001). The relationship between the TZCF and loggerheads is further examined here with comparison between the quarterly loggerhead latitude-frequency distribution and the mean quarterly surface chlorophyll density by latitude, estimated from SeaWiFS, pooled from 1997 to 2001, and averaged over the region 160°E-140°W (Fig. 4). These plots indicated that during all quarters a substantial portion of the loggerhead distribution included the TZCF as indicated by the sharp gradient in surface chlorophyll centered on the mean 0.2 mg m⁻¹ (Fig. 4). Further there was agreement between the seasonal north-south movement of the region of sharp chlorophyll gradient and the seasonal shift in the latitudinal distribution of the loggerhead positions. However, a substantial portion of the latitudefrequency distribution was located south of the TZCF

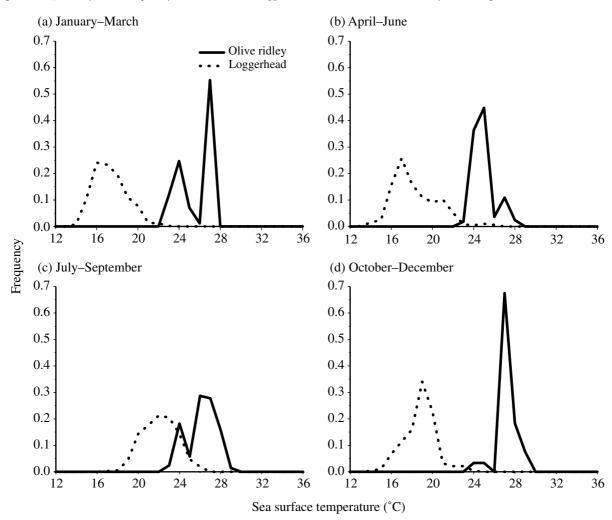


Figure 3. Quarterly SST-frequency distributions for loggerheads (dashed) and olive ridleys (solid), pooled for 1997–2001.

in all quarters (Fig. 4). For olive ridleys, satellite remotely sensed surface chlorophyll data indicated that they inhabited stratified surface waters with a fairly uniform surface chlorophyll of about 0.1 mg m⁻³ and were not associated with strong surface chlorophyll gradients.

The vertical habitat use of loggerheads and olive ridleys was examined with data from the two loggerheads and two olive ridley turtles outfitted with depth recorders. These transmitters collected information on the time-at-depth distribution binned in 6-h periods for preset depth bins. Pooled, the two loggerhead turtles reported 8888 dives over a range between 23 and 37°N during June–January. The olive ridleys reported 1118 dives between 15 and 26°N during July–October. While there was spatial and temporal variation in diving patterns for each species, consistent differences in dive depth distribution occurred

between species. Both loggerheads exhibited relatively dives and their pooled cumulative time-at-depth frequency distribution indicated that they spent 40% of their time at the surface and about 90% of their time at depths <40 m (Fig. 5). Both olive ridleys exhibited deeper diving than the loggerheads, and their pooled cumulative time-at-depth frequency distribution indicated that they spent only about 20% of their time at the surface and about 40% of their time deeper than 40 m (Fig. 5). The cumulative dive depth-frequency distributions showed patterns similar to the time-at-depth (Fig. 5). The cumulative daily maximum depth-frequency distributions also indicated that olive ridleys dive deeper than loggerheads. For example, on only about 5% of the days did loggerheads dive deeper than 100 m while olive ridleys dove deeper than 150 m at least once a day during 25% of the days (Fig. 5). As the deepest

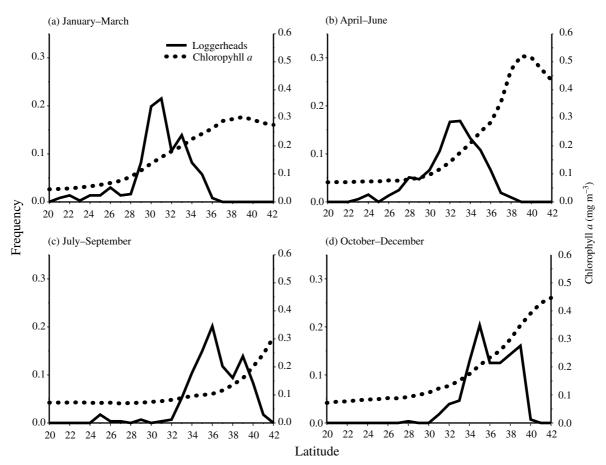


Figure 4. Quarterly latitude–frequency distributions for loggerheads (solid) and surface chlorophyll density from SeaWiFS by latitude averaged over 1997–2001 and between 160°E and 140°W longitude (dashed).

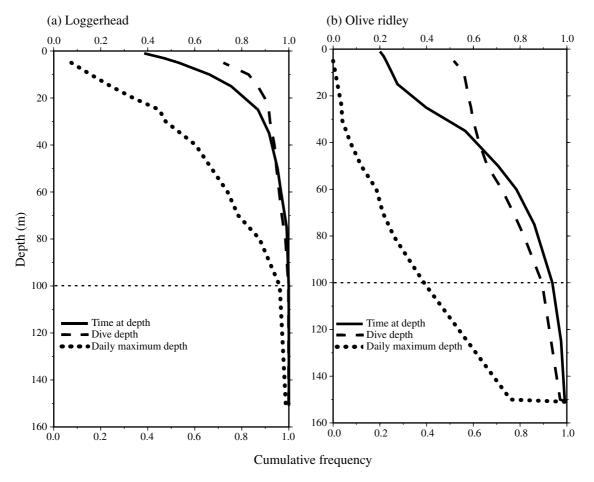
depth bin was 150 m, it is not known how deep the turtles dove below 150 m.

The Wildlife Computer dive depth transmitters did not record temperature; however, temperature and chlorophyll profiles as a function of depth were available from two oceanographic surveys. One survey in April 1998 provided a meridional depth section north of Hawaii, covering 25-34°N latitude, the region of loggerhead habitat, and reaching the TZCF at 32°N latitude (Fig. 6). The second survey in April 2001 provided a depth section south of Hawaii from 10 to 22°N latitude, including much of the region of olive ridley habitat and reaching the North Equatorial Current (NEC) at about 10°N (Fig. 6). The temperature-depth profiles indicated important differences between the thermal structure in the loggerhead and the olive ridley habitats. The olive ridley habitat was characterized by a deep thermocline at 100 m and minimal horizontal surface temperature fronts (Fig. 6). In contrast, the loggerhead habitat was characterized

by a shallow thermocline at 50 m and several strong horizontal surface temperature fronts at 20 and 17°C located at 28 and 32°N, respectively (Fig. 6). Similar depth differences in the chlorophyll-depth profiles were also observed, with the subsurface chlorophyll maximum above 100 m in the loggerhead habitat and reaching the surface at 33°N when it became the TZCF, a key feature for loggerhead habitat (Fig. 6). In the region of olive ridley habitat between 12 and 22°N latitude, the chlorophyll maximum was deeper than 100 m, although it shoaled to the surface at 10°N latitude at the northern edge of the NEC (Fig. 6).

Among the 26 loggerheads and 10 olive ridleys, one loggerhead and one olive ridley were remarkable in having transmitters that worked much longer than those of all the other turtles in their groups and hence provided our longest movement data. The loggerhead (60.0 cm SCL) traveled over 9000 km during 458 days, more than twice the distance of any other loggerhead, and the olive ridley (52.0 cm SCL)

Figure 5. Time-at-depth, dive depth, and daily maximum dive depth cumulative frequency distributions for all time periods combined: (a) both loggerheads combined, and (b) both olive ridleys combined.



traveled 7282 km in 193 days, also more than twice the distance traveled by any other olive ridley (Fig. 7). While many turtles caught in the longline fishery were hooked in the mouth, externally hooked, or entangled, the observer was able to remove the hook before releasing the animal. However in both these turtles the hooks were deeply ingested, so they were released without removal of the hooks. The tracks of these two turtles were further noteworthy in exhibiting some interesting behavior which we will further examine beginning with the loggerhead.

First, this loggerhead track very clearly showed the north–south movement also observed in the quarterly latitude–frequency distributions earlier. In March it was at 30°N latitude, reaching 40°N latitude in September, and returning back to 33°N latitude by December, while also traveling westward (Fig. 7). Secondly, during the 6-month period, December 2000 through May 2001, this loggerhead traveled predominately westward along 33°N latitude, west of the

dateline along the southern edge of the very energetic eastward flowing Kuroshio Extension Current (KEC) located at 35°N (Fig. 7). The track line of the loggerhead turtle over the 6-month period is shown together with sea surface height (SSH) and geostrophic currents estimated from Topex/Poseidon satellite altimetry for 10-day periods in February, March and April (Fig. 8). The KEC is shown as strong eastward flowing current along 35°N, associated with the sharp gradient in SSH, and the turtle track line shows the turtle's westward trajectory just south of the strong eastward KEC (Fig. 8). The turtle's westward movement was often assisted by the westward flow on the north side of the counter-clockwise rotating eddies it encountered along 33°N (Fig. 8). During February-April 2001, the loggerhead position, as indicated by the black dots on the track line, was along the edge of a KEC meander. During February, March and April this meander developed into a cyclonic eddy, and the turtle occupied the edge of the eddy (Fig. 8). These

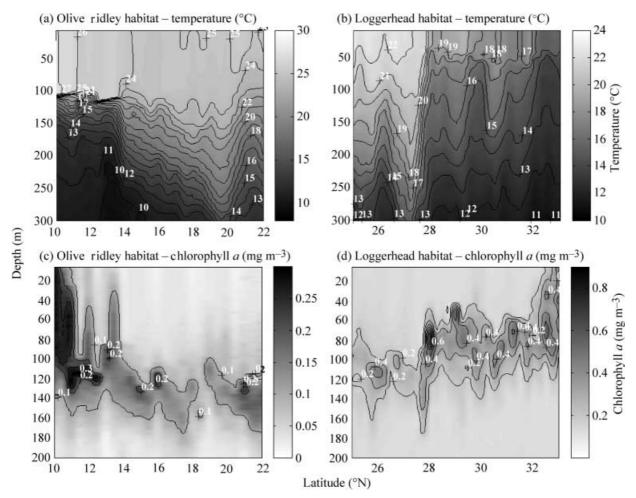


Figure 6. Temperature depth and chlorophyll depth plots for (a) olive ridley habitat (10–22°N latitude, April 21–30, 2001), and (b) loggerhead habitat (25–34°N latitude, April 24–May 1, 1998).

meanders and eddies represent regions of enhanced surface chlorophyll as seen from surface chlorophyll estimated from SeaWiFS data for February 2001 (Fig. 9). The two cyclonic eddies at 165 and 180°E and the meander at 170°E seen in the altimetry data for February 12–22 are regions of enhanced surface chlorophyll (Fig. 9). The loggerhead remained for 3 months along the edge of the meander and eddy at 170°E which represents surface convergence zones and a likely site of concentrated prey for the loggerhead (Figs 8 and 9).

The olive ridley traveling the longest distance was identified as having hatched on a western Pacific nesting beach. This turtle also went westward from Hawaii well past the dateline and showed some north—south movement as well (Fig. 7). As it headed westward, this turtle dipped south in December and January and for 40 days rode westward on the NEC (Fig. 10). While in the NEC it traveled westward at an

average speed of 71 cm s⁻¹ (SE 12 cm s⁻¹, N = 73) compared with an average speed of 48 cm s⁻¹ (SE 6 cm s⁻¹, N = 37) outside the NEC. The speed of the NEC at the daily positions of the olive ridley during its 40 days in the NEC, estimated from Topex/Poseidon satellite altimetry, was 32 cm s⁻¹ (SE 3 cm s⁻¹). When the olive ridley was in the NEC it traveled at about 71 cm s⁻¹ and as the NEC traveled at only 32 cm s⁻¹, the turtle appeared to be actively swimming and not just drifting as it rode the NEC.

This olive ridley is not the only one to use the equatorial currents. A second olive ridley, the easternmost track line in Fig. 1, used both the Equatorial Counter Current (ECC) and the NEC. It traveled eastward along the eastward-flowing ECC in September and then north and westward during October and November in the NEC (Fig. 11). The two olive ridleys that used the NEC and the ECC were identified from genetic analysis to be of western Pacific origin. The

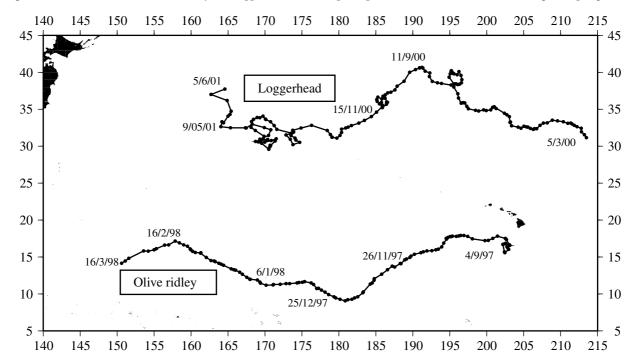


Figure 7. Track lines for the olive ridley and loggerhead exhibiting the greatest distance traveled for each species group.

third olive ridley of western Pacific origin is also associated with strong currents; it is the north-western most olive ridley in Fig. 1 and occupied the southern edge of the KEC. None of the olive ridleys of eastern Pacific origin exhibited any association with strong currents.

DISCUSSION

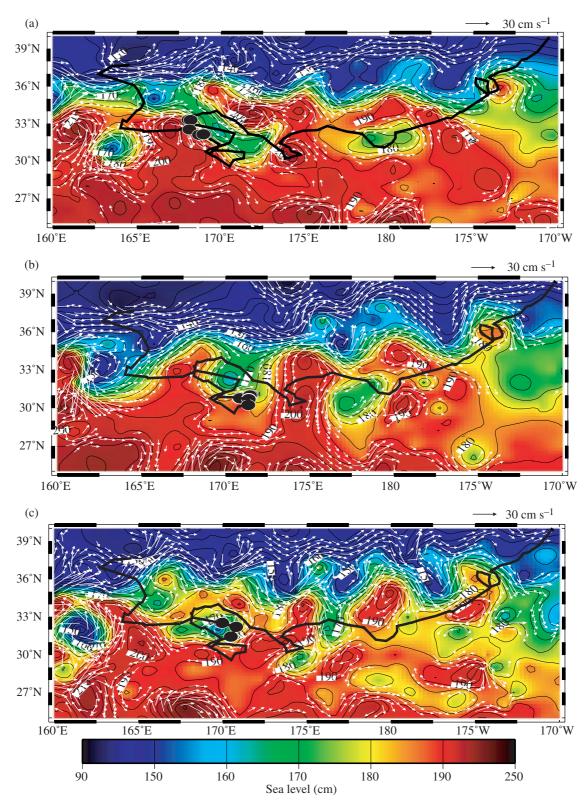
Loggerhead and olive ridley turtles occupy habitats with different physical and biological characteristics and as a result utilize different types of forage and migration habitat. Loggerheads occupy the northern edge of the Subtropical Gyre and the Transition Zone, waters characterized by a shallow thermocline, strong thermal and chlorophyll gradients, and surface convergent fronts. As a result they tend to have a relatively shallow dive depth distribution, spend considerable time at the surface, and associate with eddies and fronts including the TZCF and the southern edge of the KEC. Stomach analyses from 53 loggerheads caught in the high-seas drift net fishery in the central North Pacific further support our conclusion that loggerheads are utilizing surface convergent forage habitat (Parker et al., 2002). Their most common prey are floating organisms and organisms riding on floating objects. These include the predatory gastropod Janthina sp. and its prey Vellela vellela (By-the-wind sailor),

gooseneck barnacles, *Lepas* sp., and the pelagic crab *Planes cyaneus* which ride on logs, floats and often *V. vellela* (Parker *et al.*, 2002). The only common diet item not found exclusively at the surface was the heteropod *Carinaria cithara* (Parker *et al.*, 2002).

The loggerhead SST frequency distributions do not show the bimodal pattern with peaks at 17 and 20°C, indicative of thermal fronts, observed in the earlier analysis of tracking data with nine loggerheads during 1997–1998 (Polovina *et al.*, 2000). An examination of the SST frequency-distributions for each of the 26 loggerheads in this study found that turtles do frequently stay within a narrow SST range for the duration of their transmission. However, there are enough differences between these individual SST frequency modes so that when pooled over 26 turtles a smoother distribution results. It is likely that loggerheads occupy surface fronts, but there is a range of SSTs associated with these fronts over the broad spatial and temporal range encountered in this expanded study.

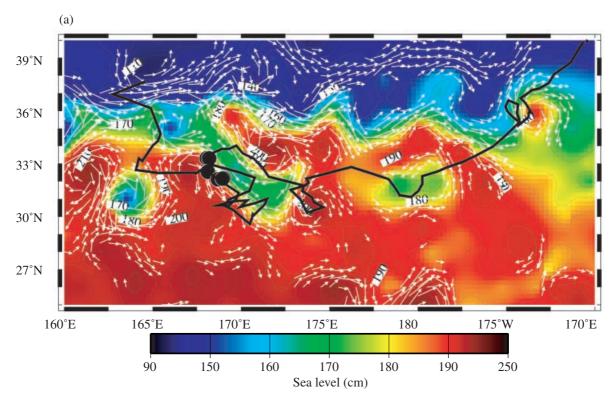
The quarterly latitude–frequency distribution based on 26 loggerheads provides evidence that loggerheads occupy the TZCF throughout the year. This confirms and expands earlier work with fewer loggerheads during winter and spring – that TZCF was an important forage habitat representing a convergence zone where cool plankton-rich water from the north converges and sinks beneath warmer nutrient-poor water to the

Figure 8. Geostrophic currents and sea surface height estimated from Topex/Poseidon satellite altimetry together with the track line and positions (dots) of the loggerhead turtle for (a) February 12–22, (b) March 13–23, and (c) April 12–22, 2001. The Kuroshio Extension Current is apparent as the strong eastward flow at 35°N.



© 2004 Blackwell Publishing Ltd, Fish. Oceanogr., 13:1, 36–51.

Figure 9. Geostrophic currents and sea surface height estimated from Topex/Poseidon satellite altimetry with loggerhead track line and positions (dots) for February 12–22, 2001 (top). Surface chlorophyll estimated from SeaWiFS ocean color together with loggerhead track line and positions (dots) for February 12–22, 2001 (bottom).



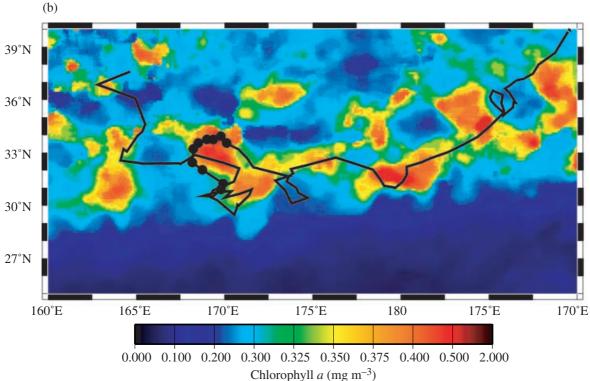
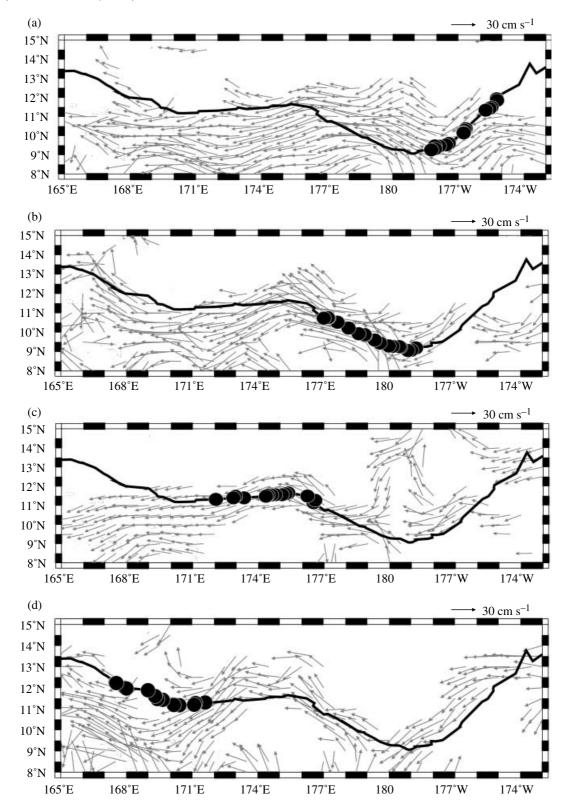
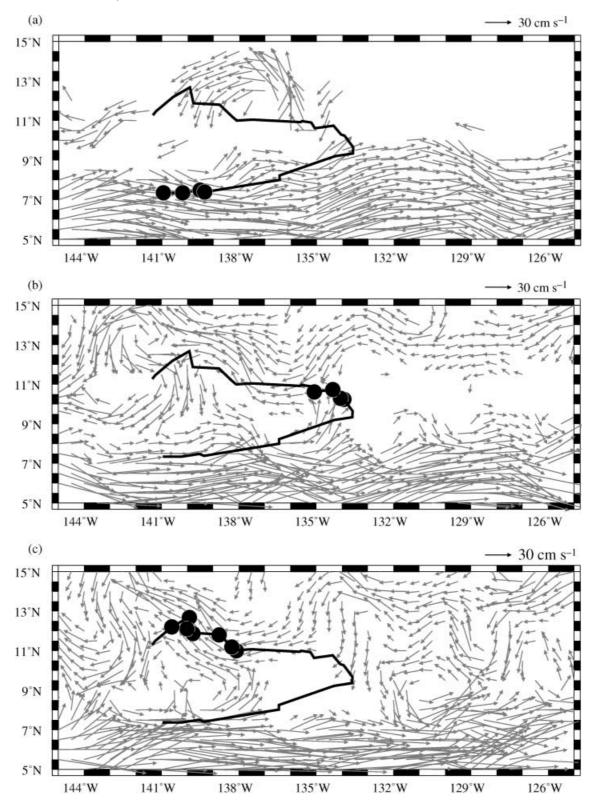


Figure 10. Geostrophic current along the North Equatorial Current estimated from Topex/Poseidon satellite together with olive ridley track line and positions (dots) for: (a) December 9–19, 1997, (b) December 19–29, 1997, (c) December 29, 1997–January 8, 1998, and (d) January 8–18, 1998.



© 2004 Blackwell Publishing Ltd, Fish. Oceanogr., 13:1, 36–51.

Figure 11. Geostrophic current estimated along the North Equatorial Current and the Equatorial Counter Current from Topex/ Poseidon satellite together with olive ridley track line and positions (dots) for: (a) September 11–21, (b) October 11–21, and (c) October 31–November 10, 1997.



south (Polovina et al., 2000). Loggerheads also occupy the region just south of the TZCF in considerable abundance, and this is also consistent with earlier work indicating that another convergent front south of the TZCF, without a surface chlorophyll signature, was also habitat for loggerheads (Polovina et al., 2000). All the fronts in this region, including the TZCF, have cooler, denser water at the northern edge and warmer, lighter water on the southern edge, resulting in a gradient in SSH that generates a weak eastward-flowing geostrophic current which the loggerheads swim against as they travel westward. It has been estimated that the speed of the opposing current at these fronts is about one-seventh of the loggerhead's mean swimming speed (Polovina et al., 2000).

The loggerhead's seasonal migration from about 30°N in the winter, reaching 40°N in the summer, and returning to 30°N latitude by the next winter, represents a round-trip movement of about 2000 km and occurs while the turtles are also traveling westward. This north-south seasonal movement is also observed in the TZCF as well as in many Transition Zone species including squid, albacore, and pomfret (Shimazaki and Nakamura, 1981; Murata, 1990; Polovina et al., 2001). While two of our easternmost loggerheads traveled south-east, all the remaining 24 loggerheads traveled westward. No loggerheads were observed heading directly east. Perhaps these turtles stay in the western Pacific until they mature and then nest in Japan. Alternatively, they may migrate eastward again before they mature, perhaps passing well north of Hawaii during the summer when the Hawaii fishery is not longlining in the area.

The southern edge of the KEC may be a very important forage habitat for turtles. While we observed only one loggerhead in this region, it remained in the region for 6 months. Several other loggerheads were heading toward this region before transmissions ended. In addition, the northernmost olive ridley we observed spent 2.5 months in this region during June-August. As the chlorophyll data suggest, this region may be productive because the strong meanders from the KEC entrain deep cool, productive waters rich in nutrients and possibly a biological community from the northern side of the KEC into cyclonic eddies. The counter-clockwise circulation of these eddies creates upwelling at the center and convergence at the edge where the buoyant prey of loggerheads would likely concentrate. Our tracking data show that loggerheads occupy the edge of these features for months. Archival tagging of juvenile bluefin tunas, which forage near the surface,

found that the southern edge of the KEC centered at about 33°N latitude between 140 and 180°E was an important habitat of juvenile bluefin from December through June (Inagake *et al.*, 2001).

Olive ridleys inhabit two different oceanic regions. Most of the olive ridleys tracked remained in the center of the Subtropical Gyre characterized by warmer more vertically stratified water with a deeper thermocline without strong surface thermal and chlorophyll gradients. In this habitat, they spend less time at the surface and have a deeper depth distribution than loggerheads. An analysis of stomach contents from eight olive ridleys caught in the Hawaii-based longline fishery indicates that while they do forage on some surfaceassociated organisms including *Janthina* sp. and cowfish (Lactoria diaphana), their most common prey are pyrosomes (Pyrosoma atlantica) and salps (Salpidea), which are found subsurface (unpublished data, Honolulu Laboratory, NMFS). Similar dietary preference has been described for olive ridleys in the eastern tropical Pacific (Kopitsky et al., in press). Thus the diet data, while very limited, are consistent with our dive data suggesting that olive ridleys tend to forage deeper than loggerheads. The amount of time olive ridleys spend at 27°C SST reflects the fact that, south of Hawaii, the distance between SST isotherms is very wide and that olive ridleys can move over a range of several degrees of latitude and still remain in 27°C SST water. For example, the olive ridley shown in Fig. 7 spent 90% of its time at 27°C SST although it moved through 5° of latitude.

In addition to inhabiting stratified Subtropical Gyre waters, three olive ridleys occupied a different habitat consisting of major oceanic currents. One traveled along the southern edge of the KEC at the north boundary of the Subtropical Gyre while two traveled in the equatorial region south of the Subtropical Gyre using the NEC and ECC. In addition to the strong geostrophic currents, the equatorial region is also characterized by wind-induced upwelling and a shoaling of the thermocline, possibly allowing the olive ridleys to forage more shallowly and in regions of surface convergences. An obvious advantage of this habitat is the strong zonal currents, which can provide substantial energetic advantages to turtles traveling east and west. The olive ridley that used the NEC to travel westward past the dateline rode the current for 40 days, almost doubling its speed in the process, and then it departed the current and headed north. It is interesting that while in the NEC the turtle did not simply drift passively but apparently swam, most likely to continually find needed prey.

The reduction of incidental catches of sea turtles in pelagic fisheries is an important management goal. In the Hawaii-based longline fishery, longlines are either set shallow, <100 m depth, to target swordfish or deep, at depths >100 m, to target bigeve tunas. Observer data, covering about 5% of the fishery effort, found that all the incidental catches of loggerheads occurred on shallow sets. Thus, in March 2001, to reduce incidental catches of loggerheads, management regulations were enacted that prohibited shallow longline sets in the Hawaii fishery. Our cumulative depth-frequency distribution for loggerheads provides further evidence that the elimination of shallow sets will substantially reduce the incidental catches of loggerheads. Secondly, the findings that the TZCF, the southern edge of the KEC, the NEC and ECC represent important forage habitat for loggerheads and olive ridley suggest that reducing fishing effort in these areas will also reduce the incidental take of these turtles.

Finally, our analyses show the value of combining satellite remote-sensed and ship-based physical and biological data with tracking data to further understand the oceanic habitat of pelagic animals and their movement patterns. This approach should prove useful in identifying oceanic marine-protected areas designed to protect pelagic animals in their spawning and foraging habitats (Hyrenbach *et al.*, 2000).

ACKNOWLEDGEMENTS

We wish to acknowledge the NMFS observers who deployed the transmitters on all the turtles; Shawn K. Murakawa and Shandell Eames who assisted in training observers and handling logistics; Robin LeRoux and Erin LaCasella, NMFS La Jolla Laboratory assisted with genetic analysis. The SeaWiFS data used in this study were produced by the SeaWiFS Project at Goddard Space Flight Center. These data were obtained from the Goddard DAAC under the auspices of NASA. Use of these data is in accord with the SeaWiFS Research Data Use Terms and Conditions Agreement. We acknowledge Dr Otis Brown, RSMAS, University of Miami, for the MCSST data. These data were obtained from the NASA Physical Oceanography Distributed Active Archive Center at the Jet Propulsion Laboratory/California Institute of Technology. We acknowledge the Laboratory for Satellite Altimetry, NODC, NESDIS, NOAA as the source for the TOPEX/Poseidon altimetry data. Finally, we acknowledge the improvements made as a result of reviews by Dr David Hyrenbach and Dr David Welch.

REFERENCES

- Balazs, G.H., Miya, R.K. and Beavers, S.C. (1996) Procedures to attach a satellite transmitter to the carapace of an adult green turtle, *Chelonia mydas. Proceedings of the 15th Annual Symposium on Sea Turtle Biology and Conservation*. US Dept. Commerce, NOAA Technical Memo. NOAA-TM-NMFS-SWFSC-37, pp. 21–26.
- Bowen, B.W., Abreu-Grobois, F.A., Balazs, G.H., Kamezaki, N., Limpus, C.J. and Ferl, R.J. (1995) Trans-Pacific migration of the loggerhead turtle (*Caretta caretta*) demonstrated with mitochondrial DNA markers. *Proc. Natl. Acad. Sci.* 92:3731–3734.
- Dutton, P.H., Balazs, G.H. and Dizon, A.E. (1999) Stock ID of sea turtles caught in the Hawaii-based longline fishery. In: Proceedings of the 17th Annual Symposium on Sea Turtle Biology and Conservation. US Dept. Commerce, NOAA Technical Memo. NOAA-TM-NMFS-SEFSC-415, pp. 43–44.
- Hyrenbach, K.D., Forney, K.A. and Dayton, P.K. (2000) Marine protected areas and ocean basin management. Aquat. Conserv.: Mar. Freshw. Ecosyst. 10:437–458.
- Inagake, D., Yamada, H., Segawa, K., Okazaki, Nitta, A. and Itoh, T. (2001) Migration of young bluefin tuna, *Thunnus orientalis*, through archival tagging experiments and its relation with oceanographic conditions in the western North Pacific. Bull. Nat. Res. Inst. Far Seas Fish. 38:53–81.
- Kopitsky, K.L., Pitman, R.L. and Dutton P.H. (in press) Aspects of olive ridley, Lepidochelys olivacea, feeding ecology at sea in the eastern tropical Pacific. In: Proceedings of 21st Annual Sea Turtle Symposium. US Dept. Commerce, NOAA Technical Memo.
- McClain, E.P., Pichel, W.G. and Walton, C.C. (1985) Comparative performance of AVHRR-based multichannel sea surface temperatures. JGR 90:11587–11601.
- McClain, C.R., Cleave, M.L., Feldman, G.C., Gregg, W.W. and Hooker, S.B. (1998) Science quality of SeaWiFS data for global biosphere research. Sea Technol. 39:10–17.
- Mitchum, G.T. (1996) On using satellite altimetric heights to provide a spatial context for the Hawaii Ocean Time-series measurements. Deep-Sea Res. 43:257–280.
- Murata, M. (1990) Oceanic resources of squids. Mar. Behav. Physiol. 18:19–71.
- National Marine Fisheries Service and US Fish and Wildlife Service (1998) Recovery Plan for US Pacific Populations of the Olive Ridley Turtle (Lepidochelys olivacea). Silver Spring, MD: National Marine Fisheries Service, 52 pp.
- O'Reilly, J.E., Maritorena, S., Mitchell, B.G. et al. (1998) Ocean color chlorophyll algorithms for SeaWiFS. J. Geophys. Res. 103:24937–24953.
- Parker, D.M., Cooke, W. and Balazs, G.H. (2002) Dietary components of pelagic loggerhead turtles in the North Pacific Ocean. In: Proceedings of the Twentieth Annual Symposium on Sea Turtle Biology and Conservation, February 29–March 4, 2000, Orlando, FL. US Dept. Commerce, NOAA Technical Memo. NMFS-SEFSC. 417:148–151.
- Polovina, J.J., Kleiber, P. and Kobayashi, D.R. (1999) Application of TOPEX/Poseidon satellite altimetry to simulate transport dynamics of larvae of spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands, 1993–1996. Fish. Bull. **97:**132–143.
- Polovina, J.J., Kobayashi, D.R., Ellis, D.M., Seki, M.P. and Balazs, G.H. (2000) Turtles on the edge: movement of

- loggerhead turtles (Caretta caretta) along oceanic fronts in the central North Pacific, 1997–1998. Fish. Oceanogr. 9:71–82.
- Polovina, J.J., Howell, E., Kobayashi, D.R. and Seki, M.P. (2001) The Transition Zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progr. Oceanogr.* **49:**469–483.
- Shimazaki, K. and Nakamura, S. (1981) Ecological studies of the pomfret (*Brama japonica*) I. The seasonal distribution pattern and ecological considerations. *Res. Inst. North Pac. Fish.*, *Hokkaido Univ.*, Special vol.: 91–103 (in Japanese with English abstract).